

## BREEDING ECOLOGY OF TAWNY AND YELLOW-BELLIED WREN WARBLERS (*PRINIA SUBFLAVA* AND *P. FLAVIVENTRIS*)<sup>1</sup>

LU-SHIH LIN<sup>\*2</sup>, PAUL S. ALEXANDER<sup>\*</sup>  
and LUCIA LIU SEVERINGHAUS<sup>\*\*</sup>

<sup>\*</sup> Graduate Institute of Biology, Tunghai University,  
Taichung, Taiwan 40704, Republic of China

<sup>\*\*</sup> Institute of Zoology, Academia Sinica,  
Taipei 11529, Taiwan,  
Republic of China

(Accepted October 5, 1987)

Lin Lu-Shih, Paul S. Alexander and Lucia Liu Severinghaus (1988) Breeding ecology of tawny and yellow-bellied wren warblers (*Prinia subflava* and *P. flaviventris*). Bull. Inst. Zool., Academia Sinica 27(1): 57-66. Populations of *Prinia subflava* and *P. flaviventris* were observed from January 1984 to May 1985 in an area of about 200 hectares in central Taiwan (Lat. 24°11'N; Long. 120°35'E) at an elevation of 150 m. The breeding activities of 68 pairs of *P. subflava* and 27 pairs of *P. flaviventris* were observed from April to September 1984. Most breeding of *P. subflava* occurred from August and of *P. flaviventris* from May to July.

The vegetation of *P. flaviventris* habitats was denser than that of *P. subflava* habitats. The main nesting sites for both species were on *Panicum maximum* and secondarily on *Miscanthus floridulus*. *P. subflava* nests were placed 42% higher than *P. flaviventris* on *Panicum* and 29% higher on *Miscanthus* grass.

The average clutch size of *P. subflava* (4.35) was larger than that of *P. flaviventris* (3.87). The egg size of *P. subflava* was slightly smaller than that of *P. flaviventris*. The mean hatching and fledging success for *P. flaviventris* were higher than those for *P. subflava*, but the greater mean number of clutches of *P. subflava* compensated for lower productivity per nest. These data suggest that the two species of *Prinia* maintain their population levels by different adaptations.

**Key words:** Breeding ecology, *Prinia subflava*, *Prinia flaviventris*.

*P. subflava* and *P. flaviventris* occur sympatrically in the lowlands of Taiwan. Aggression between the two species has been observed. The habitats of the two species appear very similar. Neither species has received prior scientific attention in Taiwan. Although both species are widely distributed in south to southeast Asia, and

*P. subflava* even in Africa, there is very little in the literature on the biology of either species. This study focuses on an analysis of their habitat characteristics and their breeding biology.

### MATERIALS AND METHODS

The study site was an area of about 200

1. Paper No. 302 of the Journal Series of the Institute of Zoology, Academia Sinica.
2. To whom reprint request should be sent.

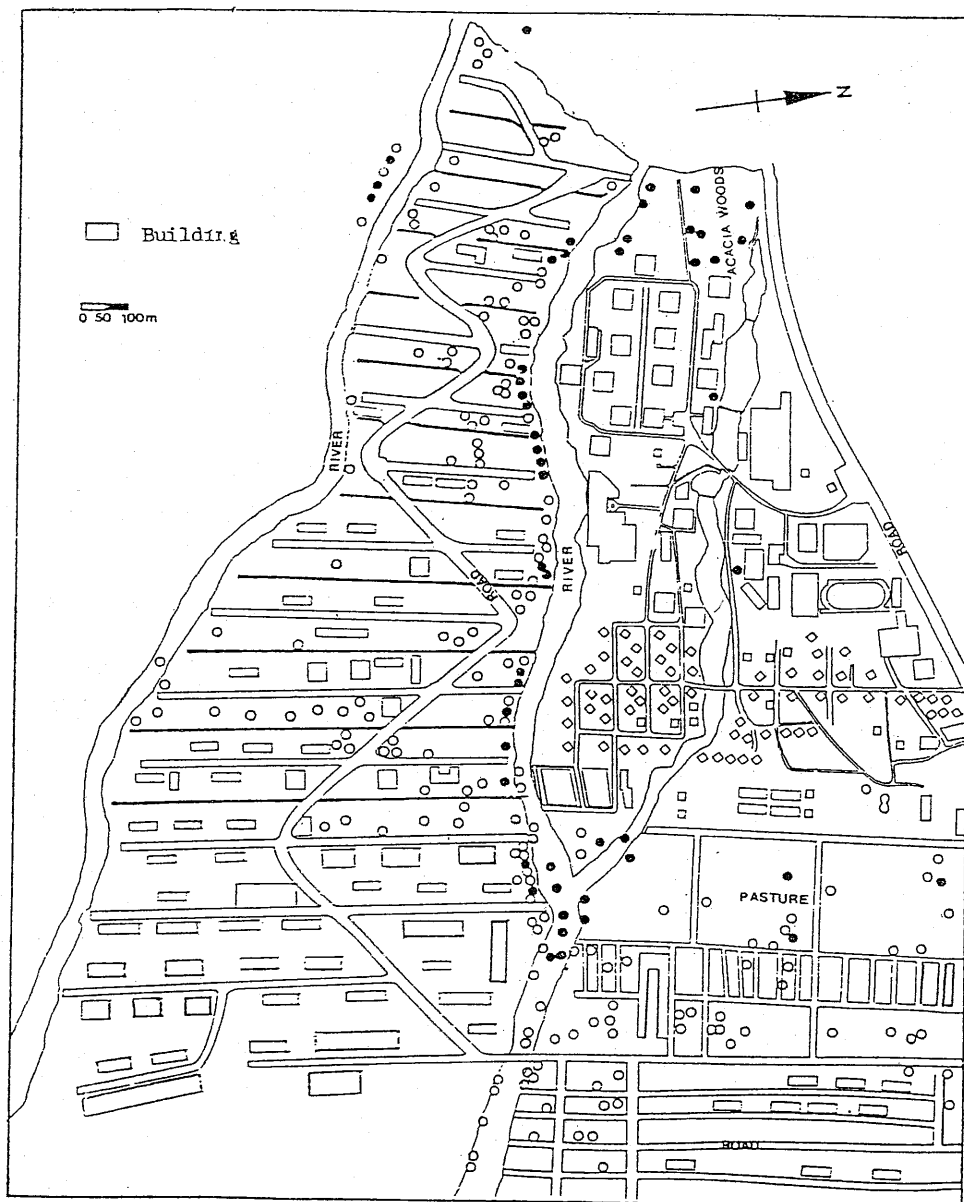


Fig. 1. Map of study area. ○ *P. subflava* nest, ● *P. flaviventris* nest.

hectares covering parts of the Tunghai University campus and the adjacent Taichung Industrial Zone (Fig. 1). Mist nets were used for 10–15 days each month from March 1984 to April 1985 (except for September to November) to capture birds for color banding. Daily observation of color-banded breeding birds and their fledglings were used to define the breeding territory. Between March and September 1984, an effort was made to

locate nests of both species. For each nest, data collected include clutch size, time of hatching, number of nestlings and time of fledging. The time of nest initiation for a nest found before incubation began was calculated on the assumption that eggs were laid at the rate of one egg per day. Such nests were visited daily or on alternate days until egg laying ceased. For nests found after incubation began, the time of nest

initiation was estimated on the additional assumption that the hatching of the last nestling was 12 days after laying of the last egg. Incubation time was calculated from the last-laying day until hatching was completed. In order to know the incubation time and the hatching success, each nest was visited on the tenth day after the beginning of incubation and then each day until all the nestlings were hatched. Since some eggs may be destroyed during incubation period, the analysis of hatching success includes data only for the clutches which were observed for ten days or more before hatching.

Hoyt's equation (1978)  $W = KLB^2$  (L=length, B=breadth, W=weight) was used to estimate egg weights. Egg length and breadth were measured at an early stage in incubation. To calculate the constant (K) in the equation, a sample of eggs were measured in the laboratory within a couple of hours after they were laid, using an electronic balance sensitive to 0.0001 g for weight. The growth curve equations for nestlings were fitted according to Ricklefs's method (Ricklefs 1967).

The spatial and vertical characteristics of vegetation in the nesting territories of 12 pairs of *P. subflava* and 9 pairs of *P. flaviventris* were surveyed in June and July 1984. The methods used were adapted from Paszkowski (1984). Within a radius of 50 m from each nest, three 1 m<sup>2</sup> plots were selected to measure the height and coverage of grasses and forbs, three 16 m<sup>2</sup> (4×4 m) plots for the height and coverage of shrubs, and three 100 m<sup>2</sup> (10×10 m) plots for the height and number of trees. One plot for each of these three categories included the nest at the center, and the other two plots for each category were selected randomly. The characteristic of herbs and shrubs were compared for their height, quadrat coverage, relative coverage, and relative frequency. The quadrat coverage for a species was calculated as the average proportion of the area covered by that species in all plots surveyed. The relative coverage for a species

was calculated as a proportion of the total quadrat coverage for all species of the same category (herbs or shrubs). The unit density of a tree species was calculated as the average number of trees of that species found in a 100 m<sup>2</sup> plot. Population size was estimated early in the breeding season by direct counting of breeding pairs.

## RESULTS

### I. Habitat survey

*Panicum maximum*, *Panicum repens*, *Miscanthus floridulus*, *Imperata cylindrica* and *Rhynchelytrum repens* are the five dominant herbs in the habitat of *P. subflava*, totaling 63.07% of relative coverage. *Panicum maximum* and *Miscanthus floridulus* were the two dominant herbs in the habitat of *P. flaviventris*, totaling 80.02% of relative coverage. *Lantana camara* and *Urena lobata* were the two dominant shrubs, totaling 70.68% of relative coverage in the habitat of *P. subflava*, whereas, *Lantana camara* and *Clerodendron cyrtophyllum* were the two dominant shrubs, totaling 70.93% of relative coverage in the habitat of *P. flaviventris*. *Acacia confusa* was the dominant tree in the habitat of both *Prinia*.

In *P. subflava* habitat, the quadrat ground coverage by herbs was 82.89%; in *P. flaviventris* habitat, it was 81.37%. The two are similar. But for shrubs, the quadrat ground coverage by shrubs of *P. subflava* habitat was 12.71%, much lower than the 22.30% of *P. flaviventris* habitat. Most birds of both species build nests on grasses. As a result, the plots around the nests had higher quadrat ground herb cover and less shrubs than plots away from the nests.

The data for quadrat coverage by herbs and shrubs of varying heights are presented in Table 1. The vegetation heights of herbs and shrubs were delineated into five categories: 50 cm, 50–100 cm, 150–200 cm, and 200 cm. The quadrat coverage of herbs and shrubs of *P. subflava*

TABLE 1  
The quadrat coverage (%) of nesting habitat by vegetation of varying height

Species	Vegetation	Height (cm)					Total
		<50	50-100	100-150	150-200	>200	
<i>P. subflava</i>	grasses	14.06	38.06	9.81	15.42	5.56	82.91
	shrubs	2.11	2.89	1.76	3.78	2.15	12.69
	total	16.17	40.95	11.57	19.20	7.71	95.60
<i>P. flaviventris</i>	grasses	9.26	10.33	14.56	34.63	12.59	81.37
	shrubs	0.41	1.15	4.48	9.52	6.74	22.30
	total	9.67	11.48	19.04	44.15	19.33	103.67

Chi-square analysis of the quadrat coverage by varying height of the two species was:

$$\chi^2=37.49, df=4, p<0.01.$$

The quadrat coverage (%) =  $\frac{\sum_{n=1}^N \% \text{ cover of a given vegetation height}}{N \times 3 \text{ plots} \times 100}$ , when  $N$  is the total number of nets sampled.

habitat was greatest for the 50-100 cm category (40.95%), whereas that for *P. flaviventris* habitats was greatest for the 150-200 cm category (44.15%). The quadrat ground coverage by herbs and shrubs of varying height differed significantly ( $\chi^2=37.49$ ,  $df=4$ ,  $p<0.01$ ) in the habitats of the two species, with greater average height of vegetation for *P. flaviventris* habitat. The unit density of trees in the habitats of *P. subflava* (1.78) was lower than that of *P. flaviventris* (7.37).

## II. Breeding territories

In April 1985 females of both species were found to occupy the same breeding territory in two consecutive years (*P. subflava* seven cases, *P. flaviventris* two cases). The mean feeding territory of 13 pairs of *P. subflava* during the breeding season in 1984 was 10,439 m<sup>2</sup> (5,137-21,000 m<sup>2</sup>). The mean feeding territory of 3 pairs of *P. flaviventris* was 4,290 m<sup>2</sup> (2,592-6,980 m<sup>2</sup>). This difference is not statistically significant ( $t=2.088$ ,  $p>0.05$ ).

If a nest is lost before the fledging of the young, females of both species may build another nest and lay another clutch of eggs. For *P. subflava*, the highest number of clutches laid per season was 4, for *P. flaviventris* it was 2. The mean distance between nests belonging to the same female

was 44.8 m ( $n=27$ ) for *P. subflava* and 32.4 m ( $n=2$ ) for *P. flaviventris* ( $t=0.555$ ,  $p>0.05$ ). The mean inter-nest distance between different pairs breeding at the same was 87.3 m ( $n=19$ ) for *P. subflava*, and 75.1 m ( $n=8$ ) for *P. flaviventris* ( $t=0.952$ ,  $p>0.05$ ).

## III. Population size

In April 1984 the population of *P. subflava* and *P. flaviventris* were 172 and 68 respectively. In December 1984 the population of *subflava* and *P. flaviventris* were 159 and 69 respectively, showing no significant change. However, in April 1985 the population of *P. subflava* and *P. flaviventris* decreased to 90 and 48 respectively. Some parts of the *Acacia* woods in the campus were cut down for building construction and some parts of Taichung Industrial Zone were also used for factory building. Fire destroyed two hectares of habitat. In addition, grass, shrubs and trees were cut in some areas for military or for better drainage in the ravine.

Between January and March 1985, the recovery rate for birds banded in March-August 1984 was 42.42% for *P. subflava* and 37.50% for *P. flaviventris*. For yearlings the recovery rate for *P. subflava* was 10.73% and for *P. flaviventris* 12.77%. The recovery rates of yearlings for the two species did

not differ significantly ( $\chi^2=0.018$ ,  $df=1$ ,  $p>0.05$ ).

#### IV. Breeding biology

##### A. Nest location

In the *Acacia* woods of the campus only nests of *P. flaviventris* were found, and in the more open Industrial Zone only nests of *P. subflava* were found. In the ravine between the *Acacia* woods and Industrial Zone the two species maintained overlapping territories (Fig. 1).

All together we found 173 *P. subflava* nests and 38 *P. flaviventris* nests. *P. subflava* nests were mostly placed on *Panicum maximum* (70%), *Miscanthus floridulus* (8%), *Acaia confusa* (7%), *Saccharum spontaneum* (5%) and *Imperata cylindrica* (4%). *P. flaviventris* nests were primarily on *Panicum maximum* (66%) and *Miscanthus floridulus* (31%). There was one nest on *Pennisetum pureum*. On *Panicum maximum*, the mean nest height above ground for *P. subflava* ( $98 \pm 12$  cm) was significantly higher than that of *P. flaviventris* ( $69 \pm 21$  cm) ( $t=5.614$ ,  $df=78$ ,  $p<0.01$ ). On *Miscanthus floridulus*, *P. subflava* also nested significantly higher above the ground ( $126 \pm 22$  cm) than *P. flaviventris* ( $98 \pm 18$  cm) ( $t=3.40$ ,  $df=23$ ,  $p<0.01$ ).

##### B. Breeding season, clutch size and success

The breeding season of both species was from April to September in 1984. However, the major breeding period for *P. subflava* was from April to August, longer than that of *P. flaviventris*, from May to July (Table 2,3). The mean date of clutch initiation from April 1 to May 31 for *P. subflava* ( $\bar{x}=32.56 \pm 17.42$ ,  $no=52$ ) was not significantly earlier than that for *P. flaviventris* ( $\bar{x}=39.08 \pm 12.82$ ,  $n=13$ ) ( $t=1.263$ ,  $df=63$ ,  $p>0.05$ ). For *P. subflava*, the mean clutch initiation date for segregated areas ( $\bar{x}=28.32 \pm 16.08$ ,  $n=19$ ) was not significantly earlier than that for the overlapping area ( $\bar{x}=35.00 \pm 17.93$ ) ( $t=1.343$ ,  $df=50$ ,  $p>0.05$ ). For *P. flaviventris*, the mean clutch initiation date for the overlapping area ( $\bar{x}=38.73 \pm 13.98$ ) was not significantly earlier than that for segregated area ( $\bar{x}=41.00 \pm 2.83$ ) ( $t=0.221$ ,  $df=11$ ,  $p>0.05$ ).

*P. subflava* may have up to 4 clutches in a breeding season while *P. flaviventris* has only two clutches. None of the nests with only one egg was incubated for either species. Hence the clutch size of one egg was omitted from the following analysis.

In the first half of the breeding season (April-June) the modal clutch size of *P. subflava* was 5, but in the second half of the

TABLE 2  
The distribution of clutch size of *P. subflava* by month in 1984

Month	Clutch size			Mean $\pm$ S. D.	N
	2-3	4	5		
April	1(1)	4(6)	10(12)	4.60 $\pm$ 0.63 (4.58 $\pm$ 0.61)	15(19)
May	3(4)	5(10)	10(19)	4.28 $\pm$ 1.02 (4.39 $\pm$ 0.86)	18(33)
June	0(0)	4(6)	11(20)	4.73 $\pm$ 0.46 (4.77 $\pm$ 0.43)	15(26)
July	3(5)	10(15)	5(14)	4.11 $\pm$ 0.68 (4.26 $\pm$ 0.71)	18(34)
Aug.-Sept.	0(6)	14(25)	1(2)	4.07 $\pm$ 0.26 (3.88 $\pm$ 0.49)	15(33)
Total	7(16)	37(62)	37(67)	4.35 $\pm$ 0.71 (4.34 $\pm$ 0.71)	81(145)

- The numbers of each clutch size include the clutches with known laying date and those without known laying date but under observation more than ten days before hatching. Numbers in parenthesis include all nests found with eggs and/or nestlings. Only 2 nests were found with 2 eggs in May.
- Data for clutch size 2 and 3 and month August and September were combined for  $\chi^2$  analysis.
- The  $\chi^2$  tests of independence of 81 nests and 145 nests for clutch size and laying month revealed that clutch size was related to the laying month ( $\chi^2=27.424$ ,  $df=8$ ,  $p<0.01$ ;  $\chi^2=38.758$ ,  $df=8$ ,  $p<0.01$ ).

TABLE 3  
The distribution of clutch size of *P. flaviventris* by month in 1984

Month	Clutch size			Mean±S. D.	N
	2-3	4	5		
April	1(1)	1(1)	0(0)	3.50±0.71(3.50±0.71)	2(2)
May	2(4)	1(3)	3(7)	4.00±1.26(4.14±1.03)	6(14)
June	1(1)	1(2)	1(1)	3.67±1.53(3.75±1.29)	3(4)
July	0(0)	3(8)	0(0)	4.00 (4.00)	3(8)
Aug.-Sept.	0(1)	1(3)	0(0)	4.00 (3.50±1.00)	1(4)
Total	4(7)	7(17)	4(8)	3.87±0.99(3.94±0.88)	15(32)

- The numbers of each clutch size include the clutches with known laying date and those without known laying date but under observation more than ten days before hatching. Number in parenthesis include all nests found with eggs and/or nestlings. In May and June, there was a nest found with 2 eggs respectively. In September there was a nest found with 2 nestlings.
- Data for clutch size 2 and 3 and month August and September were combined for  $\chi^2$  analysis.
- The  $\chi^2$  test of independence for 15 nests for clutch size and laying month revealed that clutch-size was not related to the laying month ( $\chi^2=8.214$ ,  $df=8$ ,  $p>0.05$ ), but for 32 nests revealed that clutch size was related to the laying month ( $\chi^2=16.123$ ,  $df=8$ ,  $p<0.05$ ).

breeding season (July–September) the modal clutch size became 4. Most birds nested early in the season, thus the modal clutch size for the whole breeding season was 5. The modal clutch size of *P. flaviventris* for the entire breeding season was 4, lower than the 5 of *P. subflava*. The average clutch size of *P. subflava* (4.35) was also significantly higher than that of *P. flaviventris* (3.87) ( $t=2.447$ ,  $df=94$ ,  $p<0.05$ ).

We found 145 *P. subflava* nests with eggs and/or nestlings. Only 81 of these nests had known laying dates or had been observed for more than 10 days before eggs hatched. Analyzing the relationship between clutch size and laying month, we found that clutch size calculated for either 81 nests or all 145 nests decreased significantly by laying month ( $\chi^2$  test of independence,  $p<0.01$  in both cases). We found 32 *P. flaviventris* nests with eggs and/or nestlings, but only 15 had known laying dates, or had been observed for more than 10 days before hatching. The same test of independence showed that clutch size was not related to laying month for the 15 nest. Yet when we analyzed the 32 nests, clutch size showed a decrease by month.

The hatching success for 81 *P. subflava*

nests (nestling 196/egg 352=55.68%) was lower than that for 15 *P. flaviventris* nests (nestling 40/egg 58=68.97%) and the fledging success for *P. subflava* (fledging 57/egg 352=16.19%) was also lower than that for *P. flaviventris* (fledging 16/egg 58=27.59%). When excluding nests with no success, the hatching success for 54 *P. subflava* nests (nestling 196/egg 232=84.48%) was still lower than that for the 10 *P. flaviventris* nests (nestling 40/egg 43=93.02%).

The fledging success for 103 *P. subflava* nests (fledging 138/nestling 381=36.22%) was lower than that for 23 *P. flaviventris* nests (fledging 41/nestling 83=49.40%). The number of fledgling per nest of *P. subflava* (0.70,  $n=81$ ) was lower than that of *P. flaviventris* (1.07,  $n=15$ ). The fledging success of *P. subflava* was 42.35% in the segregated area and 29.73% in the overlapping area. For *P. flaviventris*, it was 77.78% in the segregated area and 41.54% in the overlapping area. The fledging success of both species was significantly greater in the segregated areas than in the area where they had overlapping territories.

Egg predation during the incubation period was greater for *P. subflava* (31.53%)

TABLE 4  
Loss of eggs and nestlings for *P. subflava* and *P. flaviventris*

Species	Total no. eggs	Eggs robbed (%)	Eggs deserted (%)	Eggs unhatched (%)
<i>P. subflava</i>	352	111(31.53)	5(1.42)	36(10.23)
<i>P. flaviventris</i>	58	11(18.96)	0	3( 5.17)

Species	Eggs failing due to weather (%)	Nestlings robbed (%)	Nestlings died (%)	Fledglings (Fledging success)
<i>P. subflava</i>	4(1.14)	133(37.78)	6(1.71)	57(16.19%)
<i>P. flaviventria</i>	4(6.90)	22(37.93)	2(3.45)	16(27.59%)

than for *P. flaviventris* (18.96%) (Table 4).

#### C. Egg size and incubation

The egg length of *P. flaviventris* ( $15.9 \pm 0.4$  mm  $n=44$ ) is significantly greater than that of *P. subflava* ( $15.7 \pm 0.7$  mm  $n=168$ ). Similarly the egg width of *P. flaviventris* ( $11.9 \pm 0.4$  mm) is significantly greater than that of *P. subflava* ( $11.5 \pm 0.5$  mm). However, the weight of 5 fresh eggs of *P. flaviventris* (1.0945 g) was not significantly heavier than that of 14 fresh eggs of *P. subflava* (1.0676)

( $t=0.473$ ,  $df=17$ ,  $p>0.005$ ).

The constant in the egg weight equation is 0.502 for *P. subflava* and 0.507 for *P. flaviventris*. Using these constants, we calculated the weight of 44 eggs belonging to 10 female *P. subflava*. These egg weights are correlated with the female body weights ( $r=0.438$ ,  $p<0.01$ , Fig. 2). For *P. flaviventris* the correlation between the body weight of 3 females and the weight of 14 eggs is not significant ( $r=0.498$ ,  $p>0.05$ ). The range of incubation period of *P. subflava* (11–16 days)

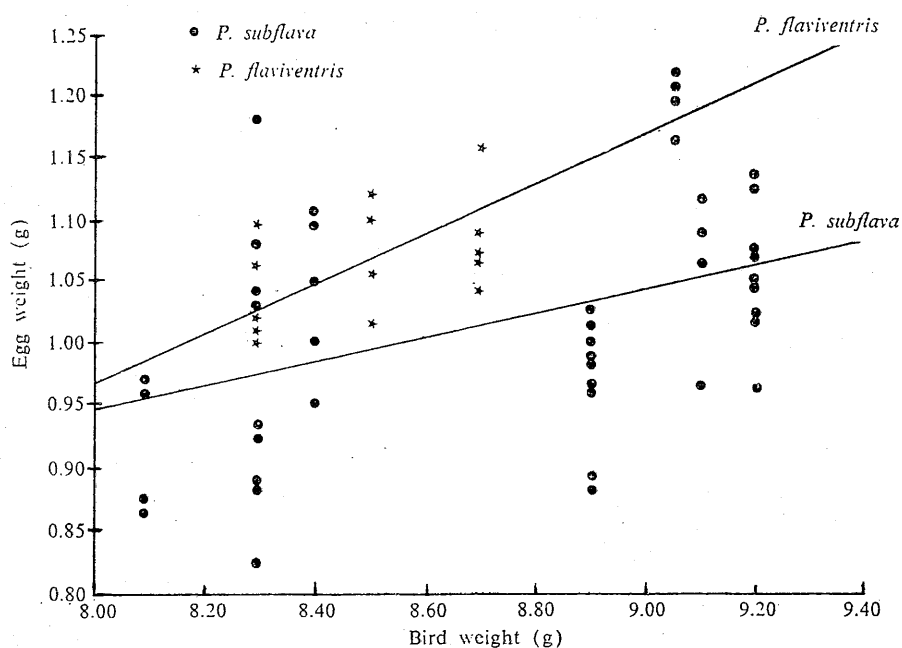


Fig. 2. The correlation of the egg weight and the female bird weight of *P. subflava* and *P. flaviventris*.

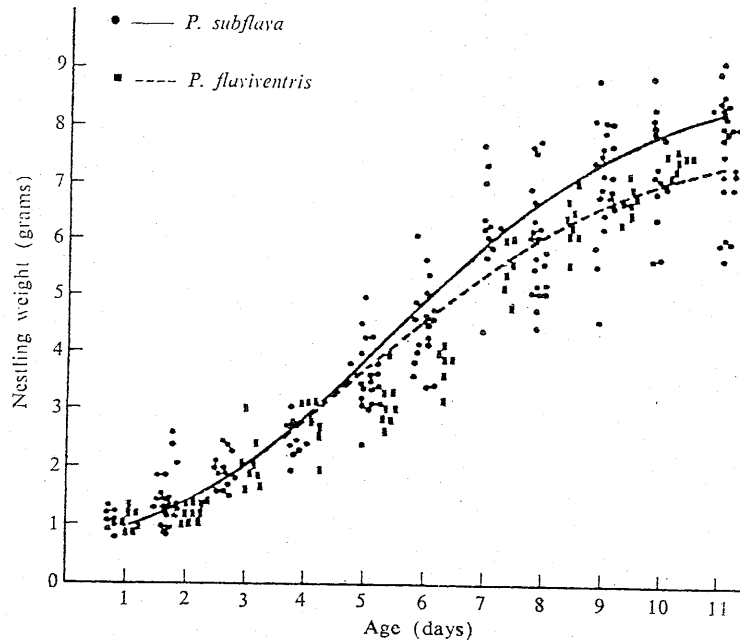


Fig. 3. Changes in weight of nestling *P. subflava* and *P. flaviventris* in 1984.

is greater than that of *P. flaviventris* (12–15 days) for this study. The mean incubation period of *P. subflava* (12.89 days) is not significantly shorter than that of *P. flaviventris* (13.29 days) ( $t=0.865$ ,  $df=33$ ,  $p>0.05$ ).

#### D. Development of the nestlings

Both nestlings of *P. subflava* and *P. flaviventris* are altricial. The changes in weight of nestlings are presented in Fig. 3. The body growth of both species is a typical logistic curve. Hatching is designated as day 1. At hatching, the nestlings weigh an average of  $1.05 \pm 0.14$  g ( $n=14$ ) and  $1.19 \pm 0.19$  g ( $n=5$ ) for *P. subflava* and *P. flaviventris*, respectively. Following Ricklefs's method (1967) the formula for the logistic curve of *P. subflava* is

$$W = \frac{8.83}{1 + e^{-0.472(TW - 5.6)}},$$

whereas that of *P. flaviventris* is

$$W = \frac{7.87}{1 + e^{-0.460(TW - 5.4)}}.$$

In these equations,  $W$  is the weight of nestlings in grams on day  $TW$ . 8.83 and 7.87

are the asymptotic weights, achieved by the average nestling of *P. subflava* and *P. flaviventris*, respectively;  $e$  is the base of the natural logarithm; 0.472 and 0.460 are the constants, proportional to the specific rate of growth of *P. subflava* and *P. flaviventris*, respectively; and 5.6 and 5.4 are the ages in days at the point of inflection on the growth curve. From the above data, we know the asymptotic weight of fledgling *P. subflava* is higher than that of *P. flaviventris*. *P. subflava* nestlings grew faster than that of *P. flaviventris*. The time interval for growth from 10 to 90% of the asymptote for *P. subflava* (9.31 days) is shorter than that of *P. flaviventris* (9.55 days), but the mean nestling period for *P. subflava* (12.4 days, range 11–14 days) is significantly longer than that of *P. flaviventris* (11.3 days, range 11–12 days) ( $t=2.497$ ,  $df=11$ ,  $p<0.05$ ).

## DISCUSSION

### 1. Habitat use and competition

*P. flaviventris* is more secretive than *P.*



*subflava*. The former prefers denser habitat with taller vegetation and the latter prefers more open area. *P. subflava* uses more species of plants for rest sites than does *P. flaviventris*.

The statistical comparison of the dates of clutch initiation for both species of *Prinia* shows no significant difference. Nests of both species in the overlapping areas had the lowest breeding success. Data suggest that breeding began about one week earlier for *P. subflava*. The earlier clutch initiation for *P. subflava* in the segregated areas suggests either preference for the more open habitat of the segregated areas or some competition with *P. flaviventris* for the overlapping areas. For *P. flaviventris*, later clutch initiation in the segregated *Acacia* woods may be attributed to the preference for the nesting territories in the overlapping ravine area and the subsequent movement of less dominant males to the *Acacia* woods. Therefore there could be competition for nesting territories, if the two species did not use different habitat.

Because of different preferences for habitat, clearing the land for most agricultural use should have a greater impact on loss of habitat for *P. flaviventris*.

## 2. Breeding and success

In Taiwan, the two species are very similar morphologically, ecologically and behaviorally. Yet, *P. subflava* produced larger clutches and more clutches per season than *P. flaviventris*, Pianka (1976 in Richter 1984) pointed out that, under the constraint of a fixed level of parental resources committed to reproduction, there should be a trade-off between more offspring of lesser quality and fewer off-spring of higher quality. The larger number of clutches and greater clutch size for *P. subflava* compensates for its lower fledging success, whereas the higher fledging success of *P. flaviventris* compensates for the smaller number of clutches and clutch size.

In addition to clutch size and clutch

number, the egg weight of *P. flaviventris* is slightly heavier than that of *P. subflava* and the incubation period of *P. flaviventris* is also slightly longer than of *P. subflava*. This positive correlation found in our study is consistent with the hypothesis that incubation period is strongly and positively correlated with egg weight (Rahn and Ar 1974 in Baersma 1982). Furthermore, the hatchling weight and growth rate of the young also suggest that *P. flaviventris* tend to invest more in each offspring in favor of higher success per offspring. More comparative studies of *P. subflava* and *P. flaviventris* in other areas where the two species are sympatric are needed to understand their interaction.

There is very little published data for breeding biology on either species. In Pietermaritzburg, South Africa, Earle (1981) reported the clutch size of *P. subflava* was 2-4 eggs and mean clutch size was 3.5 and 3.2 in 1978 and 1979, respectively. Whereas the clutch size of *P. subflava* of this study was 2-5 and mean clutch size was 4.35, higher than the clutch size in the Pietermaritzburg. In Pietermaritzburg, the modal clutch was 4 in 1978, 3 in 1979, lower than the 5 of Taiwan *P. subflava*. In Pietermaritzburg, the fledging success was 21.1% in 1978 and 27.6% in 1979 higher than the 16.19% of our study. In Pietermaritzburg, the mean number of fledglings per nesting attempt was 1.5 in 1978, 0.6 in 1979, whereas our study was 0.70. Earle (1981) hypothesized that the lower breeding productivity of 1978 in Pietermaritzburg was a result of less rainfall, which resulted in fewer arthropods being available. Although we cannot compare the rainfall between Taiwan and pietermaritzburg, because Earle did not give rainfall data, we doubt that the low productivity of Taichung area was a result of the same reason. Further study comparing different populations of *P. subflava* in Taiwan may elucidate the factors governing its reproductive success on Taiwan.

**Acknowledgements:** We thank Dr. Chung-kuei Wang and Dr. Shan-hsiung Lin for advising us on habitat survey techniques and helping with plant identification. We are grateful to Dr. Wesley Keh-chin Sun, Dr. Vivian V. Cheng Yang for advice and encouragement. We also wish to thank Mr. Pei-yi Li, Miss Shu-hua Chang, Mr. Cheng-ieh Yao and Mr. Chi-hsin Hsiao for their assistance in the field work.

### REFERENCES

- BOERSMA, P. D. (1982) Why some birds take so long to hatch. *Amer. Natur.* **120**: 733-750.
- EARLE, R. A. (1981) Factors governing avian breeding in Acacia Savana, Pietermaritzburg, part 3: breeding success, recruitment and clutch size. *Ostrich* **52**: 235-243.
- HOYT, D. F. (1979) Practical methods of estimating volume and fresh weight of bird eggs. *Auk* **96**: 73-77.
- RICKLEFS, R. F. (1967) A graphical method of fitting equations to growth curves. *Ecology* **48**: 978-983.
- PASZKOWSKI, C. A. (1984) Macrohabitat use, microhabitat use, and foraging behavior of the Hermit Thrush and Veery in a northern Wisconsin forest. *Wilson Bull.* **96**: 286-292.

## 臺灣中部褐頭鷦鶯與灰頭鷦鶯之繁殖生態

林路拾 歐保羅 劉小如

野外觀察褐頭鷦鶯和灰頭鷦鶯之繁殖生態，自民國七十三年一月起至七十四年五月止。實驗區設於臺灣中部東海大學校園附近，面積約二百公頃。七十三年四月至九月計觀察到褐頭鷦鶯 68 對，灰頭鷦鶯 27 對有繁殖現象。褐頭鷦鶯之繁殖盛期為四月至八月，而灰頭鷦鶯為五月至七月。

灰頭鷦鶯棲所之植被密度較褐頭鷦鶯之植被密度高。兩種鷦鶯主要均在大忝上築巢，其次則在五節芒上。在大忝上，褐頭鷦鶯之平均巢高比灰頭鷦鶯高 42%，在五節芒上則高 29%。

褐頭鷦鶯平均每窩蛋數為 4.35 個中比灰頭鷦鶯之 3.87 個為多。褐頭鷦鶯之蛋比灰頭鷦鶯稍小。灰頭鷦鶯之孵化成功率及離巢成功率比褐頭鷦鶯高，但褐頭鷦鶯較高之平均每窩蛋數可以補救其較低之每窩離巢雛數。這些資料表示兩種鷦鶯採取不同之適應方法以維持其一定之族羣水準。